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Current patterns, habitat discontinuities and population genetic structure: the case of the kelp *Laminaria digitata* in the English Channel

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ABSTRACT: *Laminaria digitata* is the dominant species of the dense, continuous kelp stands in the English Channel and on the Atlantic coasts of France, where it is harvested for its high quality alginates. However, in spite of its ecological and economic importance, our knowledge of the level and organisation of genetic diversity in this species is scant. Here, using comprehensive hierarchical sampling and 7 microsatellite loci, we explored the roles of dispersal strategies, current regimes and habitat discontinuities in shaping genetic structure of *L. digitata* populations. Our results show that continuous, non-fragmented forests of *L. digitata* were genetically differentiated at distances greater than 10 km, despite the absence of clear population boundaries. Furthermore, a pattern of isolation-by-distance indicated that gene flow occurred preferentially among adjacent populations following a stepping-stone model. In addition, we analysed the direction of migration using assignment tests and found that currents appeared to play a minor role in orienting gene flow, except in the Gulf of Saint Malo gyre. In contrast, habitat discontinuities were found to accentuate genetic differentiation and resulted in reduced genetic variation of isolated stands. In the context of a potential over-exploitation of kelp stands in Brittany, this study suggests that the existence of neighbouring populations can be vital to maintaining high levels of gene flow and thus, genetic diversity in this species.

KEY WORDS: Seaweed · Fragmentation · Hydrodynamic models · Dispersal · Asymmetric gene flow · Assignment test

INTRODUCTION

Genetic differentiation is generally associated with dispersal mode. In marine animals, numerous studies have demonstrated that the existence of a pelagic phase — promoting dispersal over long distances — strongly influences genetic differentiation (for reviews, see Palumbi 1994, Bohonak 1999, Féral 2001). Indeed, in species with direct development, genetic differentiation occurs at smaller spatial scales than in species with planktonic larval phases (gastropods: Kyle & Boulding 2000; marine shore fishes, Waples 1987; bryozoans: Goldson et al. 2001; echinoids: Poulin & Féral 1996). Most marine algae are characterised by relatively short-lived spores and gametes (Santelices 1990). However, although they lack the strict equivalent of 'planktonic larvae' as in benthic invertebrates, drifting (detached) fertile thallus fragments occasionally constitute a mechanism for long-distance dispersal and reinforce gene flow. Although less abundant in comparison to benthic invertebrates, studies of genetic structure in seaweeds have effectively shown that genetic differentiation occurs at relatively short distances (<1 m to <10 km) and that different modes of spore

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and/or gamete dispersal resulted in different levels of genetic structure (Sosa & Lindstrom 1999, Valero et al. 2001). Indeed, in brown seaweeds, the few published population genetic studies suggest that species without floating dispersal stages show greater genetic structuring than species possessing such a stage (Lu & Williams 1994, Williams & Di Fiori 1996, Coyer et al. 1997, Kusumo & Druehl 2000, Engelen et al. 2001).

The intensity of restricted gene flow also depends on the geographic relationships between source and recipient populations. In particular, genetic differentiation should increase with geographic distance when migration is spatially restricted, as predicted under a stepping-stone model (Kimura & Weiss 1964). Thus, if dispersal is limited, isolation by distance will be detected even within continuously distributed populations. Furthermore, gene flow can be influenced by marine currents and/or discontinuities in the habitat. Genetic differentiation may not solely depend on geographic distance, but also on the orientation of currents, which can promote or prevent gene flow (rockfish: Rocha-Olivares & Vetter 1999; marine invertebrates: Wares et al. 2001; brown seaweeds: Miller et al. 2000, Engelen et al. 2001). Discontinuities in the habitat, such as river mouths, stretches of unsuitable substrate etc., can also create barriers to gene flow and favour genetic differentiation (fishes: Bernardi 2000, Riginos & Nachman 2001; snail: Johnson & Black 1998a; red alga: Faugeron et al. 2001).

Kelps (order Laminariales, Phaeophyta) are the most abundant algae in the subtidal euphotic zone of rocky coasts, from temperate to polar seas. Present only on the western coast in the North Atlantic, *Laminaria digitata* is the dominant species of the dense and continuous kelp stands on the English Channel and Atlantic coasts of France (Kain 1979). These large brown seaweeds are ecologically important in coastal environments as primary producers, important contributors to food webs and as shelters to a wide range of invertebrates (Duggins et al. 1989, Norton et al. 1996, Walker & Kendrick 1998). Kelps are not only important ecosystem engineers (Kain 1979, Coleman & Williams 2002), but they are also a main marine commercial resource for various (e.g. food, cosmetic and paint) industries as a source of gel-forming polysaccharides, known as alginates. In Brittany, natural populations of *L. digitata* are harvested for their high quality alginates (Arzel 1998). However, monitoring the production of *L. digitata* in Brittany over the past 15 yr has shown that despite increased harvesting capacities, the annual landings of *L. digitata* have been decreasing over the past 5 yr (Arzel 1998, P. Arzel pers. comm.).

In spite of its ecological and economic importance, our knowledge of the genetic resources in *Laminaria digitata* is scant. In particular, since boundaries among populations are difficult to discern, it is not known whether the *L. digitata* forest forms a single genetic entity or several genetically differentiated entities. This question is especially important in light of potential over-exploitation of *L. digitata* stands. In this study, we used 7 microsatellite loci (Billot et al. 1998) to examine the pattern of genetic diversity in stands of *L. digitata* on the North Atlantic coast and in the English Channel. Using a hierarchical sampling design (from 45 m to >100 km), we aimed to assess the effective dispersal abilities of *L. digitata* and to determine the geographic scale at which differentiation occurs. First, we explored the genetic diversity at the smallest sampling scale to examine whether mating occurs at random. Second, by comparing genetic distance with geographic distance, we compared the differentiation among the hierarchical scales and confronted this differentiation with an isolation-by-distance model. Third, we assessed the role of tidal currents and habitat discontinuities in the observed differentiation pattern. Finally, we tested the possibility of directional, current-oriented gene flow using an assignment test.

MATERIALS AND METHODS

Study species. *Laminaria digitata* is a short-lived perennial species characterised by a heteromorphic haploid-diploid life cycle (Sauvageau 1916), in which diploid sporophytes alternate with haploid gametophytes. The large, conspicuous plants (up to 3 m long) belong to the diploid sporophyte generation. These sporophyte plants produce large numbers of meiospores (zoospores), which after a planktonic stage lasting up to 72 h, settle and grow into microscopic male and female gametophytes. These in turn produce gametes by mitosis. Male gametes are released and fertilise female gametes that are retained on the female gametophyte. Following fertilisation, a new sporophyte plant develops. *L. digitata* meiospores are produced directly on the blade, the flag-like distal portion of the plant (i.e. 1 to 3 m above the substratum).

Male gamete dispersal is probably extremely limited (ca. 1 mm; Maier et al. 1988) as spermatozoids are incited to release by the pheromones produced by female gametophytes (Müller et al. 1979). Kelp dispersal is thus ensured mainly by planktonic bi-flagellate haploid spores or possibly by drifting fertile thallus fragments that continue to produce and release meiospores.

As the gametophytes are dioecious, outcrossing is obligatory. However, fertilisation between gametophytes arising from the same sporophyte, equivalent to self-fertilisation, is possible (Billot et al. 1999). Asexual or vegetative reproduction is not known *in natura* in

kelps; however, asexual reproduction (apospory) has been successful in the laboratory (Le Gall et al. 1996).

Sampling. A total of 438 diploid individuals were sampled in 1997 and 1998, from natural, non-harvested areas along the coasts of Brittany and Normandy following a hierarchical design (Fig. 1A). In all, 18 plots were grouped into 12 sites (separated by ca. 10 to 50 km) belonging to 4 regions. In 5 sites, 2 plots separated by less than 2 km were sampled. In each plot, 25 sporophytes were sampled within a 50 m^2 area, except at NB-5 (Plougrescant), where only 13 sporophytes were collected. Sampling reflects the species' distribution in the study area. In particular, plots were sampled from the continuous stands of kelps in Brittany and Normandy and from isolated stands along the shoreline delimited by unsuitable sandy substrate, as for Locquirec (NB-4) and Saint Malo (SM-1), or by land discontinuities, as for the island of Jersey (SM-2) (Fig. 1).

Current patterns in the English Channel. Arriving at the western point of Brittany, the major current, the Gulf Stream, is diverted into 2 main orientations (Fig. 1B). South of Ushant Island, currents are characterised by south-bound flow; whereas north of Ushant Island, waters entering the English Channel present an eastern-orientated flow. These waters are diverted towards the north, and, according to Salomon & Breton's tidal current model (no wind, average tidal amplitude), they follow a path off Lannion towards Plymouth (Fig. 1B; Salomon & Breton 1993). The current then separates into 2 routes, 1 westbound along the Cornwall coast towards the Scilly Islands and the other eastbound towards Normandy. The remainder of the flow forms large gyres around the islands of Jersey and Guernsey, which delimit the Gulf of Saint Malo. Although this general pattern varies with wind and with other physical factors, the Gulf of Saint Malo is always isolated from the main flow (Salomon & Breton 1993).

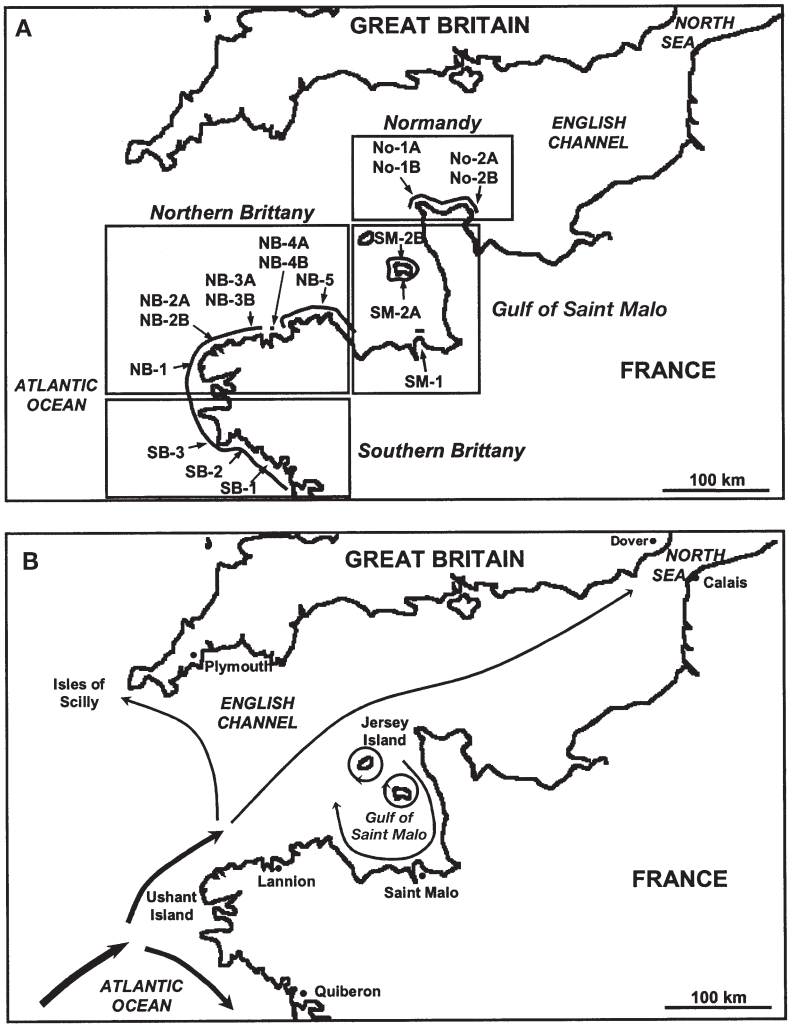

Fig. 1. *Laminaria digitata.* Geographic and hydrodynamic characteristics of sampled stands of *L. digitata.* (A) Locations of sampled plots along the coasts of Brittany and Normandy. The distribution of *L. digitata* stands in the study area is indicated by bold thick lines (Thouin et al. 1983, present study). (B) Long-term, average current trajectories in the English Channel, based on Salomon & Breton (1993) and the French Service Hydrographique et Oceanographique de la Marine

Microsatellite genotyping. The meristematic part of each thallus was cleaned of epiphytes and desiccated in silica gel until DNA extraction. DNA was extracted using Chelex (Biorad) beads according to Billot et al. (1998). Seven microsatellite loci (Ld1-124, Ld2-148, Ld2-158, Ld2-167, Ld2-531, Ld2-371 and Ld2-704) were amplified according to standard PCR protocols to genotype each individual thallus (Billot et al. 1998). Allele sizes and composition of each individual were determined using an automatic VISTRA sequencer (Molecular Dynamics) as described in Billot et al. (1998).

Data analysis. Genetic polymorphism in each plot was measured as the mean number of alleles per locus (N_a), gene diversity (H_e, sensu Nei 1978) and observed heterozygosity (H_o) using the GENETIX software package (Ver. 4.01; Belkhir et al. 1999). Allele frequencies are available upon request. Fixation indices (F_{IS}) within each plot were computed for each locus and heterozygote

deficiencies and excesses were tested using 10 000 randomisations of alleles among individuals within each plot using FSTAT (Goudet 1995).

Two-way analyses of variance (ANOVA) were performed on per-plot and per-locus H_e, N_a and F_{IS} estimates to test for the congruence of the loci and to check the occurrence of panmictic reproductive systems in each plot. The factors plot and locus were declared random and both tested over the error term, as only 1 value was observed per locus and per plot, precluding an interaction term. Differences in gene diversities and mean number of alleles were assessed using a Wilcoxon 2-sample test when comparing plots from continuously distributed stands and isolated stands.

To test for the genetic independence of the microsatellite loci, genotypic linkage disequilibria between the 21 pairs of loci were tested in each plot by performing 10 000 permutations of alleles within a locus with GENETIX software (Ver. 4.01; Belkhir et al. 1999). The proportion of permutations as high as or higher than the observed value provides an unbiased estimation of the probability that there is no linkage disequilibrium. Sequential Bonferroni correction was applied to guard against Type I error when performing multiple tests (adjusted 5% nominal level = 0.26%) (Rice 1989).

The organisation of genetic diversity was analysed using Weir & Cockerham's (1984) estimators of *F*-statistics. In this analysis, F_{IS} estimates the average deviation from random mating within plots and F_{ST} the average differentiation between plots. Genetic differentiation was also estimated at the different scales of the hierarchical sampling. First, F_{PS} measures the differentiation between plots belonging to the same site; second, pooling plots within sites, F_{SR} measures differentiation between sites within a region; finally, pooling sites, F_{RT} measures the differentiation between regions. Values and their SDs (obtained by jack-knifing over loci) were computed using the FSTAT software package (Ver. 2.9.1; Goudet 1995). The significance of the deviation of each estimator from 0 was tested using the permutation procedure included in FSTAT (10 000 randomisations).

Isolation by distance (Slatkin 1993) was tested by regressing pairwise genetic distances on the geographical distances separating sites using GENEPOP (Ver. 3.1a; Raymond & Rousset 1995). Genetic distances were measured as $F_{ST}/(1 - F_{ST})$, where F_{ST} is the multilocus estimate (Rousset 1997). Geographical distances were measured as distances along the coast for continental populations and taken as the direct distance for the Jersey site. Considering its limited bathymetric range (+1 to −5 m), *Laminaria digitata* occupies a habitat (rocky substrata along the coast) much longer than it is wide. We therefore considered that dispersal distances would be better equated to a linear (1-dimensional) distribution than a radial (2-dimensional) one (Rousset 1997); thus, linear, not log-transformed distances, were used. The correlation between matrices of genetic and geographic distances was tested using a Mantel permutation procedure (10 000 permutations) as provided in the GENEPOP software package, where the p_{Mantel} value is the proportion of permutations resulting in a correlation coefficient equal to or less than the observed value.

Assignment tests. While genetic differentiation estimated by F_{ST} informs as to the degree of differentiation among populations, assignment tests are powerful methods for identifying (recent) immigration events, even when overall differentiation among populations is low (Rannala & Mountain 1997, Waser & Strobeck 1998). Assignment tests are particularly pertinent in exploring the role of marine currents in the genetic differentiation among populations as the patterns of misclassification can be used to determine the direction of migration. The probability that *Laminaria digitata* individuals are (recent) immigrants from sites other than the site of sampling (site of 'residence') was determined using the 'Bayesian' method provided in computer program GeneClass (Cornuet et al. 1999). This method is based on Rannala & Mountain's (1997) approach that determines the likelihood of drawing a particular multilocus genotype from a resident and from a potential source site, based on the assumption that loci are independent. Individuals are assigned to the most likely population of those included in the study. All individuals are thus assigned to 1 population, whether it be the 'true' population of origin or one with the closest matching genetic signature (Cornuet et al. 1999).

Using all 12 sites, sites of residence and sites of assignment were confronted to evaluate the proportion of immigrants in each site and the origin of any immigrants. Unilateral Fisher exact tests were performed using BIOMstat Ver. 3.301 (Exeter software) to test: (1) differences in the rates of immigration between isolated and continuous stands; (2) differences in immigration and emigration rates in isolated stands; and (3) orientation of gene flow in the Channel. More specifically, these hypotheses were tested as follows. First, since isolated stands by definition exchange fewer migrants with other populations, the proportion of individuals correctly classified within their site of origin should be higher in isolated stands compared to continuous stands. Second, if each isolated stand behaves as a sink (i.e. exports few migrants), the number of emigrants out of each isolated stand (i.e. individuals collected in Northern Brittany and Normandy, but assigned to isolated stands) should be greater than the number of immigrants into those stands (i.e. individuals sampled in each isolated stand, but assigned to Normandy or Northern Brittany). Third, if there is

directional gene flow oriented from west to east in the Channel as predicted by Salomon & Breton's (1993) model, the number of emigrants from Northern Brittany to Normandy should be greater than the number of immigrants from Normandy into Northern Brittany.

RESULTS

Genetic diversity and Hardy-Weinberg equilibrium in *Laminaria digitata* populations

Numbers of alleles and gene diversity are given for each microsatellite locus and for each population in Table 1. Generally, genotypes could be determined for virtually all individuals and microsatellite loci with the exception of Locus Ld2-158, which, due to poor amplification, was undersampled in 3 populations. The number of alleles per locus ranged from 6 to 23. Mean numbers of alleles were significantly different between plots and loci (2-way ANOVA without replication, locus, $F_{6,102} = 77.63$, $p < 0.001$; plot, $F_{17,102} = 3.87$, $p < 0.001$). Mean gene diversity varied significantly between loci (from 0.43 to 0.85; Table 1), but showed only marginal differences between plots (2-way ANOVA without replication: locus, $F_{6,102} = 36.11$, $p < 0.001$; plot, $F_{17,102} = 1.97$, $p = 0.07$). Most alleles (46 out of a total of 72 alleles) were shared among Atlantic and English Channel populations, with none of them being diagnostic for the Atlantic populations.

Only 1 pair of loci (i.e. 0.3 %) showed significant linkage disequilibrium, suggesting that, in general, loci segregate independently. The lone detected locus pair in linkage disequilibrium was due to the correlation between rare alleles of Loci Ld2-158 and Ld2-167 observed in 2 individuals of the NB-2B site.

The multilocus F_{IS} estimated over the 18 sites was low, but significant ($F_{IS} = 0.07$; SD = 0.016; $p < 0.001$). This positive value indicated a slight heterozygote deficiency. However, over the 156 F_{IS} values calculated for each locus and plot, only 4 remained significant after Bonferroni correction (Table 1). F_{IS} values did not vary significantly among loci and plots (2-way ANOVA without replication: locus, $F_{6,102} = 1.45$, $p = 0.20$; plots, $F_{17,102} = 0.86$, $p = 0.62$). Finally, only 1 plot (SM-2B, Jersey) exhibited a significant multilocus F_{IS} value (0.19, $p < 0.05$).

Patterns of genetic differentiation in *Laminaria digitata* populations

Hierarchical analysis

The multilocus F_{ST} estimated using all 18 sites was highly significant, indicating that gene flow is limited in *Laminaria digitata* ($F_{ST} = 0.068$; SD = 0.011; $p < 0.001$). Hierarchical analysis revealed similarities in genetic differentiation among the 4 regions. At the lowest level of the hierarchical sampling, the low, non-significant estimates of F_{PLS} established that plots within sites were not genetically distinct, whatever the region. At the between-sites/within-region level, F_{SR} values were systematically greater than F_{PL} values and highly significant, showing a pattern of concomitant increase in genetic and geographic distances (Fig. 2). However, the degree of differentiation varied among regions. At distances of 10 to 50 km, Southern Brittany and Normandy showed differentiation (F_{SR}) weaker than that observed at 50 to 100s of km (F_{RT}) (Fig. 2). On the other hand, the F_{SR} values within Northern Brittany and the Gulf of Saint Malo regions were actually greater than that of the overall differentiation among regions (F_{RT}). These latter 2 regions both contain isolated stands (Gulf of Saint Malo: Sites SM1 and SM2; Northern Brittany: Site NB4). In addition, these isolated stands exhibited a significantly lower genetic diversity than sites sampled within the continuously distributed stands (isolated: $N_a = 5.00$, $H_e = 0.529$; continuous: $N_a = 5.43$, $H_e = 0.596$; Wilcoxon 2-sample test: N_a, $p = 0.009$ and H_e, $p = 0.04$; Plougrescant [NB5] excluded from calculations due to insufficient sample size).

Isolation by distance

An overall pattern of isolation by distance was present (regression equation: $F_{ST}/[1 - F_{ST}] = 5 \times 10^{-5}\,D + 0.063$, $R^2 = 0.034$, $p_{Mantel} = 0.016$, where D is geographic distance). First, a clear pattern was present for sites of the continuous stands from Southern Brittany, Northern Brittany and Normandy (regression equation: $F_{ST}/[1 - F_{ST}] = 7 \times 10^{-5}\,D + 0.027$, $R^2 = 0.504$, $p_{Mantel} = 0.006$; Fig. 3), suggesting that the genetic structure of these sites results from an equilibrium between genetic drift and distance-restricted migration. The relatively weak slope of the regression curve indicates that levels of gene flow were nevertheless high. Among the isolated stands (□, Fig. 3), Locquirec (NB-4) and Saint Malo (SM-1) were greatly differentiated from all other sites (F_{ST} estimates ranged from 0.08 to 0.16; details not shown). As for Jersey, differentiation between the Jersey (SM-2) and Brittany (Northern and Southern) sites fit the clear Brittany-Normandy isolation-by-distance pattern (▣ found in proximity of regression line, Fig. 3), while the differentiation between Jersey (SM-2) and Normandy was greater than expected from the isolation-by-distance pattern established using the continuous Brittany-Normandy stands.

Table 1. Genetic characteristics of *Laminaria digitata* in the English Channel and Southern Brittany. N: total number of sampled individuals; N_a: number of alleles per locus and per site; H_e: expected heterozygosity; F_{IS}: estimate of heterozygote deficiency; values in bold refer to significant values after Bonferroni correction (adjusted nominal level was 0.0004)

Region	Siteplot	Southern Brittany			Northern Brittany								Gulf of Saint Malo			Normandy			
		SB-1	SB-2	SB-3	NB-1	NB-2		NB-3		NB-4		NB-5	SM-1	SM-2		No-1		No-2	
Locus						A	B	A	B	A	B			A	B	A	B	A	B
Ld1-124	N	22	25	25	25	25	25	25	25	24	25	12	25	25	25	21	24	20	25
	N_a	4	3	4	5	5	4	4	6	4	3	3	4	3	3	3	4	3	3
	H_e	0.450	0.633	0.257	0.530	0.536	0.595	0.340	0.539	0.556	0.425	0.467	0.660	0.346	0.153	0.596	0.611	0.405	0.431
	F_{IS}	0.094	0.373	−0.091	0.019	0.030	0.06	−0.179	0.036	−0.051	0.346	0.476	0.155	0.194	−0.049	−0.288	0.115	0.139	0.073
Ld2-148	N	23	23	25	25	25	25	25	25	25	23	13	24	25	25	23	20	24	24
	N_a	4	4	4	7	7	7	7	6	5	5	4	3	5	4	6	6	5	6
	H_e	0.588	0.573	0.582	0.807	0.776	0.791	0.812	0.763	0.608	0.728	0.711	0.678	0.601	0.696	0.706	0.609	0.632	0.560
	F_{IS}	0.116	0.014	0.109	−0.092	0.230	0.040	0.066	0.111	0.081	0.227	0.139	0.017	0.137	**0.488**	0.078	0.266	0.146	−0.118
Ld2-158	N	10	11	25	25	25	25	25	25	22	18	11	18	25	25	17	19	10	22
	N_a	5	4	2	5	3	5	4	2	4	4	2	3	5	4	4	4	4	4
	H_e	0.442	0.398	0.274	0.625	0.469	0.441	0.480	0.246	0.481	0.211	0.173	0.500	0.476	0.545	0.469	0.474	0.500	0.452
	F_{IS}	−0.139	−0.149	0.127	−0.157	−0.198	−0.091	0.000	−0.143	−0.138	−0.054	−0.053	−0.115	0.077	0.046	−0.134	0.339	0.413	−0.108
Ld2-167	N	23	19	24	25	25	25	25	25	25	25	12	24	25	25	25	25	25	25
	N_a	6	7	6	7	5	6	7	7	3	4	3	2	4	3	3	5	2	2
	H_e	0.630	0.758	0.770	0.683	0.644	0.667	0.691	0.696	0.483	0.575	0.554	0.422	0.633	0.587	0.528	0.585	0.503	0.458
	F_{IS}	0.175	0.100	0.027	−0.055	0.196	−0.020	**0.368**	−0.095	0.175	−0.045	0.257	0.013	0.117	0.185	0.246	0.114	−0.116	0.217
Ld2-371	N	24	19	25	25	25	25	25	25	13	22	13	25	25	25	25	25	25	25
	N_a	10	9	12	13	12	17	13	17	7	6	11	8	11	13	11	12	10	11
	H_e	0.785	0.821	0.888	0.883	0.874	0.917	0.904	0.909	0.788	0.748	0.874	0.716	0.894	0.867	0.834	0.834	0.836	0.874
	F_{IS}	0.153	**0.365**	0.101	**0.280**	0.086	−0.093	0.072	0.032	0.126	0.029	0.033	−0.006	−0.121	0.079	−0.155	−0.057	0.044	−0.008
Ld2-531	N	22	24	24	25	25	25	25	25	22	24	13	24	25	25	24	24	15	24
	N_a	5	5	5	5	4	6	4	4	3	3	3	2	4	4	5	5	4	4
	H_e	0.735	0.744	0.739	0.674	0.536	0.586	0.610	0.708	0.210	0.356	0.655	0.503	0.732	0.701	0.779	0.752	0.752	0.744
	F_{IS}	0.010	−0.181	−0.016	−0.009	−0.045	0.115	0.15	−0.018	−0.082	0.064	0.063	0.425	0.184	0.205	0.201	0.002	0.387	−0.066
Ld2-704	N	23	25	25	25	25	25	25	25	18	21	13	19	25	25	24	23	22	18
	N_a	3	2	4	4	5	2	7	3	2	2	3	2	3	3	2	3	2	2
	H_e	0.553	0.458	0.483	0.669	0.520	0.470	0.600	0.389	0.356	0.285	0.446	0.309	0.365	0.448	0.361	0.382	0.507	0.386
	F_{IS}	0.376	0.217	0.091	0.165	0.234	0.324	0.068	−0.03	−0.259	0.167	−0.217	0.151	0.014	0.019	−0.04	−0.26	0.288	−0.008
Multi-locus	N_a	5.3	4.9	5.3	6.6	5.9	6.7	6.6	6.4	4	3.9	4.1	3.4	5	4.9	4.9	5.6	4.3	4.6
	H_e	0.598	0.626	0.571	0.696	0.622	0.638	0.634	0.607	0.497	0.475	0.554	0.541	0.578	0.571	0.610	0.607	0.591	0.558
	F_{IS}	0.079	0.109	0.050	0.010	0.073	−0.001	0.106	0.005	0.039	0.105	0.154	0.079	0.078	**0.191**	−0.005	0.108	0.174	−0.011

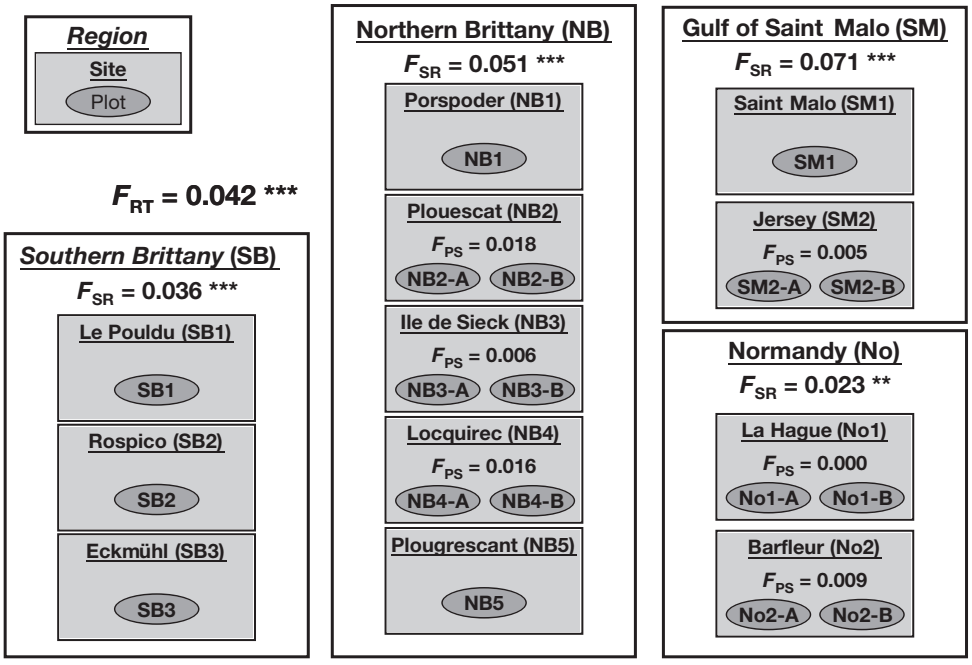

Fig. 2. *Laminaria digitata.* Hierarchical genetic differentiation of *L. digitata* populations. F_{PS}: differentiation between plots within sites; F_{SR}: differentiation between sites within a region; F_{RT}: differentiation between regions. ** and *** refer to significant values with $p < 0.01$ and $p < 0.001$, respectively, corrected by a Bonferroni test over sites in regions and plots in sites

Assignment tests

Individuals from the 12 sites were classified according to site of origin (sampling) and site of assignment (Table 2). Overall, the individuals coming from isolated sites (Locquirec: NB-4; Saint Malo: SM-1; Jersey: SM-2) were significantly better assigned to their site of residence than those sampled in continuous stands: in isolated stands, we observed 93 correctly assigned individuals out of the 125 collected individuals (74%); while in continuous stands, the ratio was 143:313 (46%) (93:32 vs 143:170; Fisher exact test, $p = 3 \times 10^{-8}$). Moreover, isolated stands tended to have higher rates of immigration than emigration from/to the neighbouring Northern Brittany and Normandy regions (SM-1: p = 0.031; SM-2: p = 0.053; NB-4: p = 0.020; adjusted 5% nominal level = 0.017).

Among continuous stands, a relatively high level of gene flow was detected among regions: 9 to 15% of migrants were detected between the central region (Northern Brittany) and its 2 neighbouring regions (Southern Brittany and Normandy). Moreover, no pattern of current-oriented gene flow could be observed in the English Channel, since as many migrants arrived from Normandy as were sent there: 14 migrants from Normandy were collected among the 138 Northern Brittany plants (10%) and 15 out of 100 individuals collected in Normandy were identified as migrants from Northern Brittany (15%) (p = 0.176).

Interestingly, among the isolated stands, the Gulf of Saint Malo sites (SM-1 and SM-2) appeared to receive more migrants from Northern Brittany than from Normandy, with Saint Malo receiving no migrants from Normandy. More strikingly, no exchange at all existed between the 2 Gulf of Saint Malo sites. Similarly, Locquirec (NB-4) did not receive any migrants from Normandy and most of the gene flow came from the Northern Brittany region.

DISCUSSION

In this study, 7 microsatellite loci revealed 72 alleles within 438 diploid *Laminaria digitata* genomes. This

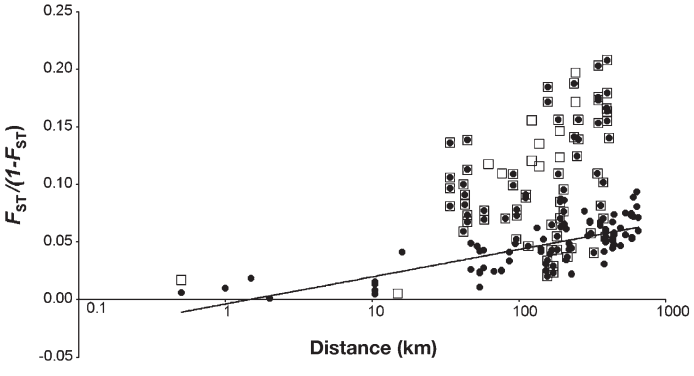

Fig. 3. *Laminaria digitata.* Genetic differentiation of *L. digitata* populations in the English Channel. Pairwise genetic distances, represented as $F_{ST}/(1 - F_{ST})$, are plotted against geographic separation distances. (●), Pairs of sites found in continuous stands; (□), pairs of sites sampled in isolated stands; (◙) pairs consisting of a continuous-stand site and an isolated-stand site

Table 2. Number of individuals assigned to each of the studied sites

	Brittany-Normandy continuum									Isolated stands		
	SB			NB				No				
Observed site	SB1	SB2	SB3	NB1	NB2	NB3	NB5	No1	No2	NB4	SM1	SM2
Predicted site												
SB1	13	6	1	0	3	0	0	1	0	0	0	2
SB2	4	12	2	1	0	0	0	0	0	1	0	0
SB3	1	3	10	2	1	5	1	0	0	3	0	5
NB1	1	1	1	13	3	2	0	2	1	0	0	1
NB2	0	0	2	2	22	11	0	4	3	2	0	3
NB3	1	0	1	1	9	14	2	3	1	0	1	2
NB5	1	0	3	0	2	1	5	1	0	4	2	0
No1	1	2	0	1	2	3	1	21	7	0	0	2
No2	2	0	2	1	3	3	0	13	33	0	0	1
NB4	0	1	1	2	0	2	1	1	2	38	0	1
SM1	0	0	1	0	1	1	2	1	0	0	22	0
SM2	1	0	1	2	4	8	1	3	3	2	0	33
Total observed	25	25	25	25	50	50	13	50	50	50	25	50
		75				138			100			

high level of genetic diversity allowed not only the analysis of population structure, but also the precise identification of migration events between populations and the direction of this migration. We have shown that, despite the absence of clear boundaries between populations, *Laminaria digitata* populations are geographically structured. Discussed below are 3 possible causes that may have generated the observed pattern of genetic diversity in and among *L. digitata* populations: (1) intrinsic life history characteristics, (2) current patterns and (3) habitat discontinuities.

Mating system and genetic differentiation: inferring dispersal patterns

Given the haploid-diploid life cycle of kelps, consanguineous mating or genetic sub-structuring can only arise from limited spore dispersal and the subsequent preferential mating between neighbouring (sibling) gametophytes. The present study suggests that most matings occurred at random in *Laminaria digitata* stands of at least 50 m^2, even if some inbreeding or spatial sub-structuring may occur in a given site (Table 1). Moreover, the consistency among loci and the absence of linkage disequilibrium showed that asexual reproduction is negligible in natural populations of *L. digitata*.

The hierarchical sampling design used in this study demonstrates that *Laminaria digitata* stands of at least 2 km constitute a single genetic entity, as plots were never significantly differentiated within sites. However, significant genetic structure was systematically observed between sites (separated by ca. 10 to 50 km). At distances greater than 10 km, even if episodic migration events (e.g. via drifting spore-bearing blades) may exist, they were not sufficient to prevent significant genetic differentiation in continuous non-fragmented stands. A clear pattern of increasing genetic distance with geographical distance revealed that gene flow, via the dispersal of spores, occurs preferentially among adjacent stands following a stepping-stone (isolation-by-distance) model within continuous non-fragmented stands.

In benthic marine invertebrates, differences in levels of gene flow have been causally linked to the mode of larval dispersal (direct development vs planktonic larvae, e.g. Knowlton & Jackson 1993, Poulin & Féral 1996, Shulman 1998). Likewise, in kelps, differences in spore dispersal are expected depending on the morphology of the species (Dayton 1985). Some stipate and prostate species such as *Macrocystis* ssp. and members of the Alariaceae family have sprorophylls at the base of the plant near the substratum which probably promotes only limited dispersal. Similarly, the sea-palm kelp, *Postelsia palmaeformis*, is characterised by drooping, deeply grooved blades which favour local recruitment by channelling and concentrating zoospores near the parental sporophyte. On the contrary, some other species, such as *Pelagophycus porra* and *Laminaria digitata* form sori at the distal end of the thallus which are far above the substratum, favouring wider spore dispersal. Differences in levels of genetic structure confirmed the difference in dispersal distances between the 'proximal' and 'distal' spore dispersal strategies. The use of dominant fingerprint-type genetic markers (M13, RAPD, AFLP) have shown limited spore dispersal by revealing strong significant genetic structuring at fine spatial scales in 2 species characterised by 'proximal' dispersal (*Alaria margi-*

nata, <15 m, Kusumo & Druehl 2000; *P. palmaeformis*, <25 m, Coyer et al. 1997). In comparison, meiospores of 2 'distal' strategy species (*P. porra*, Miller et al. 2000; *L. digitata*, the present study) disperse at distances in the order of km since significant genetic differentiation was not revealed at this scale (20 km in 'leeward' *P. porra*; 2 km in *L. digitata*).

Genetic structure and current patterns

In addition to the intrinsic dispersal strategy adopted by *Laminaria digitata*, the hydrodynamic features of the English Channel and the North Atlantic coasts of France may also shape gene flow. The dispersive properties of the currents in the English Channel, a sea featuring some of the greatest tidal amplitudes and strongest currents in the world, have been described in detail by hydrodynamic models of residual tidal currents (Salomon & Breton 1993), and applied to the dissemination of particles (Guegueniat et al. 1993) and larvae (e.g. Thiébaut et al. 1994, 1996, Barnay et al. 2003, Ellien et al. unpubl.). The existence of such a model provides a valuable opportunity to compare genetic differentiation patterns with the comprehensive information on current dynamics in Brittany and Normandy.

Using major current trajectories (Fig. 1B) to formulate hypotheses on the directionality of gene flow, offshore gene flow (i.e. between Northern Brittany and the Gulf of Saint Malo) showed the expected asymmetry: currents did orient gene flow in the Gulf of Saint Malo, effectively isolating Jersey (SM-2) and Saint Malo (SM-1) from Normandy (No-1 and No-2). However, our results reveal that currents play a relatively minor role in shaping genetic differentiation patterns of continuous coastal kelp populations. In particular, gene flow occurred among Southern Brittany and Northern Brittany *Laminaria digitata* stands in a stepping-stone fashion in spite of differences in current orientation between the English Channel and the Atlantic. Moreover, assignment tests confirmed that exchanges occurred in both directions, across the divergent currents. Furthermore, within the English Channel itself, no pattern of current-oriented gene flow was observed, since no predominant eastern-oriented flow could be detected.

While significant surface currents have been shown to shape patterns of genetic differentiation in some species (e.g. seagrass: Bandeira & Nilsson 2001; bryozoans: Goldson et al. 2001; fish: Rocha-Olivares & Vetter 1999), other studies have found no correlation (echinoderms: Palumbi et al. 1997; reef fishes: Shulman & Bermingham 1995). In this study, 2 major reasons may explain the absence of current/gene flow correlation of *Laminaria digitata* in the English Channel. First, even though it accurately describes gene flow between mainland and island populations, Salomon & Breton's (1993) model does not take into account the local turbulence regimes independent from main current trajectories created by the convoluted topography of the Brittany coast. Second, currents in the English Channel are highly dependent on wind conditions and are thus variable in time (Salomon & Breton 1993), either in intensity or even in orientation. Interestingly, however, in Salomon & Breton's (1993) model, the isolation of the Gulf of Saint Malo prevails whatever the wind conditions. Altogether, our results indicate that currents shape gene flow in kelp populations only when the major trajectories depend on neither local topography nor variable wind conditions.

Habitat discontinuities

Natural population discontinuities occur if the rocky substratum required for settlement of *Laminaria digitata* gametophytes is interrupted. Indeed, while we have shown the importance of current regimes in assuring the connection of the Jersey (SM-2) site with the Brittany continuum, Jersey nevertheless showed reduced genetic variability. Lower genetic diversity and comparatively fewer alleles were also featured in 2 other sites located in isolated stands, Locquirec (NB-4) and Saint Malo (SM-1). Thus, as predicted (see Young et al. 1996), fragmentation in species that otherwise occur naturally in large, continuous populations, generally leads to a reduction in genetic variation (Templeton et al. 1990, Young et al. 1996, 1999). This reduction arises from either a bottleneck (reduction in census population size) or from the rupture of connection with other populations (reduction in gene flow) (Young et al. 1996, Templeton 1998).

In this study, the 3 isolated sites were much more differentiated from the other sites than would be predicted by the isolation-by-distance pattern modelled on continuous stands. This increase in genetic differentiation suggests that the reduction in genetic variation in isolated sites results from reduction in gene flow with neighbouring *Laminaria digitata* stands. Indeed, in other marine species, habitat discontinuities accentuate genetic differentiation (fish: Danley et al. 2000, Riginos & Nachman 2001; red alga: Faugeron et al. 2001; marine gastropod: Johnson & Black 1998b; squid: Shaw et al. 1999). Thus, in spite of the highly dispersive nature of the marine environment, the existence of neighbouring populations can be vital to maintaining high levels of gene flow.

Implications for the harvesting *Laminaria digitata* populations

We have shown that the continuity of kelp stands was more important for gene flow than hydrodynamic regimes in 2 ways. First, we demonstrated an isolation-by-distance pattern of genetic differentiation between Southern and Northern Brittany in spite of divergent, potentially isolating, currents. Second, we revealed that habitat discontinuities accentuate genetic differentiation and, consequently, reduce genetic variation. Artificial fragmentation of *Laminaria digitata* populations is thus likely to reduce genetic variation in natural populations by rupturing contacts with neighbouring stands. Although the link between reduction in neutral genetic diversity and extinction is debated (Schemske et al. 1994), new harvesting practices may lead to the fragmentation of continuous populations beyond demographic sustainability. In the context of possible over-exploitation of *L. digitata*, the results from our study show that the risk of depletion of genetic variation and extinction should seriously be taken into account by the resource management bodies responsible for the sustainability of this marine algal crop.

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